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AN HYPOTHESIS CONCERNING THE FUNCTION OF THE METAPLEURAL GLANDS IN ANTS

The metapleural glands are organs characteristic of all ants (Formicidae), with the relatively few exceptions that are the main subjects of this note. Situated at the posterolateral corners of the alitrunk (thorax plus propodeum), the glands are marked externally by the presence of a bulla, which covers the atrium or collecting chamber, and a meatus in the form of a slit or pore that connects the atrium with the outside. Proximally, the atrium has a cribriform wall into which enter separately the ducts of single gland cells. The structure of this organ was beautifully worked out for *Myrmica* by Janet (1898), and details have been added by Tulloch (1936) for *Myrmica* and by Tulloch, Shapiro, and Hershenov (1962) for *Myrmecia nigrocincta*.

During grooming, some ant species have been seen to draw the legs, especially the tibiae and tarsi of the forelegs, repeatedly over the meatus of the gland and then to rub these leg parts over the rest of the body. One gains the impression that some substance is being spread over the integument by this means. Among various hypotheses suggested for the gland's function, one that has persisted, especially in informal conversations among ant specialists, proposes that the gland produces a "nest odor" by means of which members of one colony recognize one another. Gösswald (1953) found the gland atrophied in the female of the aberrant workerless parasitic ant *Teleutomyrmex schneideri* (it is absent in the male also) and supposed that, if the gland is connected with nest odor, its loss in *Teleutomyrmex* would be understandable in allowing easier acceptance of the parasite by the host ant species, *Tetramorium caespitum*. A rapid survey of the collection of the ants in the Museum of Comparative Zoology, Harvard University, and some other collections, has turned up additional cases of ants in which, judging now only from externally visible structures, the metapleural gland is absent, nonfunctional, or significantly reduced. It should be emphasized that the presence of a well-developed bulla and meatus, where these occur, is no guarantee that the gland cells within are present and secreting a normal product. Where the meatus is fused shut, on the other hand, the gland may safely be considered as nonfunctional.

Even as based on this wholly external criterion, the survey shows some interesting regularities in the occurrence of gland atrophy. Such cases fall into four classes:

1. Males of army ants, subfamily Dorylinae.
2. Males of a few other genera, mainly in subfamily Myrmicinae (e.g., *Leptothorax duloticus, Tetramorium, Strongylognathus, Rhoptromyrmex, Huberia striata*).
3. Workers of the specialized slave makers of genus *Polyergus*.
4. Queens of certain scattered ant species that are known (or assumed, on grounds of other morphological peculiarities) to be social parasites, i.e., those species which found their colonies in the nests of other ant species.

Class 4 includes at least the females of most of the really extreme workerless permanent social parasites, for example, *Anergates atratulus, Teleutomyrmex schneideri* (Gösswald, 1953), *Anergatides kohli, Bruchomyrma acutidens. Bregmatomyrma carnosa,* an enigmatic oriental formicine known only from the queen caste and probably parasitic, lacks bulla and meatus. Several known or assumed temporary social parasites also belong here, for example, queens of *Aphaenogaster tennesseensis* and *A. mariae* and of *Rhoptromyrmex* species (particularly *R. transversinodis*), *Chalepoxenus gribodoi* and *C. mullerianus, Myrmica colax, Lasius fuliginosus* and allied species, *Acanthomyops latipes* and *A. murphyi, Polyergus rufescens, P. lucidus,* and *P. mandarin.* However, females of a number of known or reasonably assumed parasites, both of the temporary and permanent sorts, have bulla and meatus well developed or only moderately reduced; examples are *Formica* of the *microgyna* and *rufa* groups (broad sense); *Bothriomyrmex atanticus, flavus, pusillus,* and *wroughtoni; Crematogaster atitlanica; Pseudoatta argentina; Leptothorax* (including *Formicoxenus*) *nitidulus* and *dueoticus;* all three species of *Harpagoxenus; Rossomyrmex proformicarum; Pheidole* (including *Epipheidole, Sympheidole, Eriopheidole*) *elecebra, inquilina,* and *symbiotica;* and *Myrmecia inquilina.*

In queens of the few parasitic Dacetini scattered in genera *Strumigenys, Serrastruma* and *Kyidris,* the bulla is present, but it was not possible to be sure whether the meatus was present and open, or closed. Only study of the internal parts will show whether the listed species have functional glands or not.

What do these four classes of ants have in common? For class (2), we cannot say; hardly anything is known of the behavior of most myrmicine males inside the nest or outside, and the genera named are no exceptions. But for classes (1), (3), and (4), we have an obviously common behavioral thread. All of these forms—doryline males, parasite queens, and *Polyergus* workers—must enter ant colonies other than the ones in which they were reared. In each case, unopposed entry is necessary for the survival of the entering species. Doryline males must mate with wingless queens that are closely attended by massed workers in alien nests of the same species; parasite queens must gain acceptance to avoid being killed by the workers of the host nest that will rear their brood; *Polyergus* workers, wholly dependent on captured *Formica* slaves, need to make their slave raids into *Formica* nests with minimal opposition from the adult worker inmates.

All this suggests to me a hypothesis about the function of the metapleural gland: the gland produces a substance that, when tasted or smelled, says to another ant colony, especially one of the same species, "I am an enemy." This does not require a nest odor in the sense that seems implicit in most discussions and experiments on the matter, though one would have to suppose that nest mates do not attack one another because their odor or taste is so similar that the difference signifying "enemy" does not exist. Such within-colony similarities could well be due to food sharing (trophall-

axis), mutual grooming and glossation of the body surfaces, etc., that spread colony-specific combinations of molecules around among inmates of one nest, as in the honeybees. According to the hypothesis, an individual either with the same odor-or-taste, or with none at all, would be treated by its host colony as a neutral.

Many known and suspected parasite species, both with and without external signs of a metapleural gland, have other features, such as glandular hairs and trichomes, and large smooth, polished areas of the body, that appear to attract and pacify host workers, perhaps usually through the medium of secreted liquids (*allomones,* see Postscript) smelled or tasted by the hosts. It is conceivable that such apparatus, if producing potent allomones in quantities large enough, could overcome the effects of an "enemy pheromone" produced by the same individual. In fact, the frequently ambiguous response of host workers to certain parasite queens, a response alternately hostile and amicable, could be due to the conflicting influences of attractant allomones and enemy pheromones. It is interesting to note in this connection that the parasitic female of *Acanthomyops murphyi* has a heavy mat of long, appressed golden hairs, apparently glandular, over the distorted and reduced metapleural gland area. This suggests that, even if the metapleural gland does release a product, it is fairly smothered by the thick vestiture and any secretions from the latter.

If the metapleural gland does produce a pheromone that says to other colonies of the same species, "I am an enemy," there remains the important question of how such identification can be adaptive. At the moment, we can answer this question only by pointing to the indubitable fact that individuals of most ant species normally tend to treat members of different conspecific colonies with hostility, or at least to avoid them. Also, although relatively few ants have been studied from this point of view, a number of species are known to guard and fight for territories around their nests. It therefore seems that the metapleural glands and their product(s) may serve, at least in part, as an epideictic device, or mechanism by means of which the colony as a whole senses and reacts adaptively to changes in important population parameters.

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POSTSCRIPT

Allomone: a chemical substance produced or acquired by an organism which, when it contacts an individual of *another species* in the natural context, evokes in the receiver a behavioral or developmental reaction adaptively favorable to the transmitter. The term means essentially the same as *alloiohormone* (Bethe, 1932), but is shorter and is deliberately

chosen to parallel the much-used and well-understood words *hormone* and *pheromone*. Allomone has been used in informal discussions in the United States for two or three years, and it seems to meet a need. The term grew out of conversations between T. Eisner and myself, and we are currently wondering whether a more extended treatment of the kinds and roles of allomones would be worth publishing.

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